Nonhost Angiosperm Volatiles and Verbenone Disrupt Response of Western Pine Beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae), to Attractant-Baited Traps

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ABSTRACT Nonhost angiosperm volatiles and verbenone were tested for their ability to disrupt the response of western pine beetle, *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae), to attractant-baited multiple funnel traps. Verbenone significantly reduced attraction; however, no difference was observed between 4 and 50 mg/24-h release rates. Combinations of six bark volatiles (benzyl alcohol, benzaldehyde, *trans*-conophthorin, guaiacol, nonanal, and salicylaldehyde), three green leaf volatiles [(*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol], and the nine compounds combined did not significantly reduce *D. brevicomis* response to attractant-baited traps. However, a significant effect was observed when the bark and green leaf volatiles were combined with verbenone. The nine nonhost angiosperm volatiles (NAVs) significantly augmented the effect of both release rates of verbenone, reducing trap catches to levels significantly below that of either release rate of verbenone alone. *trans*-Conophthorin, a compound reported to have behavioral activity in a number of other scolytids, was not critical to the efficacy of our NAV blend. Our results suggest that the addition of nonhost angiosperm volatiles to verbenone could be important for developing successful semiochemical-based management techniques for *D. brevicomis*.

KEY WORDS *Pinus ponderosa*, pest management, disruptant, antiaggregation pheromone, nonhost volatiles

WESTERN PINE BEETLE, *Dendroctonus brevicomis* Le-Conte (Coleoptera: Scolytidae), is a major cause of ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws., mortality in the western United States and particularly in California (Furniss and Carolin 1977). Under certain conditions, this species can aggressively attack and kill apparently healthy trees of all ages and size classes (Miller and Keen 1960). Much of this tree mortality occurs within the large-diameter (>50 cm at 1.37 m) classes. Land management objectives require the maintenance of large trees to meet the habitat requirements for several threatened, endangered, and sensitive wildlife species. Currently, pest management techniques for managing *D. brevicomis* infestations are limited to tree removals (thinning) that reduce stand density and thus host susceptibility, and the use of insecticide treatments (Wood et al. 1985). In many cases, such options are not viable for implementation because of regulatory and social constraints.

Verbenone (4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one) is an antiaggregation pheromone of several

Dendroctonus spp., including *D. brevicomis* (Borden 1997), and it is naturally derived from three sources: 1) the beetles themselves; 2) auto-oxidation of α-pinene and subsequently *cis*- and *trans*-verbenol to verbenone (Hunt et al. 1989); and 3) auto-oxidation from *cis*- and *trans*-verbenol to verbenone by microorganisms, typically yeasts, associated with bark beetle species. Verbenone was first identified in male *Dendroctonus frontalis* Zimmerman and *D. brevicomis* by Renwick (1967) and subsequently in the hindgut of emergent and feeding female *D. ponderosae* Hopkins (Pitman et al. 1969). In 1970, verbenone was demonstrated to elicit a negative response on tethered, flying *D. brevicomis* females (Hughes and Pitman 1970). Bedard et al. (1980a) showed that verbenone reduced the number of *D. brevicomis* trapped at a baited source. Trap catches were further reduced by higher release rates of verbenone (Bedard et al. 1980a, b; Tilden and Bedard 1988). It is assumed that verbenone reduces intraspecific competition by reducing the crowding of developing brood within the host (Byers and Wood 1980, Byers et al. 1984).

In recent years, verbenone has been evaluated as a tool for mitigating coniferous tree mortality due to bark beetle (Scolytidae) infestations. In western North America, efforts have concentrated on single tree or small-scale stand protection, primarily from *D. ponderosae* infestations (Amman et al. 1989, 1991;

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Lindgren et al. 1989, Gibson et al. 1991, Shea et al. 1992, Shore et al. 1992, Lindgren and Borden 1993, Progar 2003). Results have been favorable but inconsistent (Gibson et al. 1991, Shea et al. 1992), which may be due, in part, to photoisomerization of verbenone to behaviorally inactive chrysanthenone in the presence of direct sunlight (Kostyk et al. 1993). Recent field studies conducted to assess the efficacy of high release rates of verbenone (50 mg/24 h) for suppression of *D. brevicomis* infestations have had limited success (C.J.F., unpublished data).

Bark beetles often colonize one or a few closely related host-tree species (Wood 1982). Dispersing beetles must therefore discriminate among different tree species as hosts are unevenly distributed spatially and temporally in mixed forests. Volatile stimuli associated with host and nonhost trees are important in mediating such behavioral responses (Byers 1995). Scolytids are believed to use a combination of host kairomones and aggregation pheromones to locate suitable hosts (Borden 1985). Rejection of nonhosts may occur on the basis of absence of host cues or presence of nonhost cues such as green leaf volatiles or angiosperm bark volatiles, collectively termed nonhost angiosperm volatiles (Borden 1997). Nonhost angiosperm volatiles have been the focus of several recent studies that demonstrated these compounds are capable of reducing aggregation in some *Dendroctonus* spp., including *D. frontalis*, *D. ponderosae,* and *D. pseudotsugae* Hopkins (Dickens et al. 1992; Wilson et al. 1996; Borden et al. 1997; Poland et al. 1998; Huber and Borden 2001a; Huber et al. 2000b, 2003). Although there are exceptions (Huber et al. 1999, 2000a), nonhost angiosperm volatiles are usually only effective for reducing bark beetle attraction when presented in combinations of two or more compounds (Zhang and Schlyter 2004).

One study examined the effect of nonhost angiosperm volatiles on *D. brevicomis* attraction, but it was limited in scope to green leaf volatiles only (Poland et al. 1998) and was conducted at the periphery of the beetle's native range (Wood 1982). The aldehyde (*E*)-2-hexenal, and two alcohols (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol significantly reduced the number of male *D. brevicomis* caught in attractant-baited traps. (*Z*)-2-Hexen-1-ol also reduced the number of female *D. brevicomis* captured (Poland et al. 1998). In British Columbia, nonhost angiosperm volatiles and verbenone significantly reduced *D. ponderosae* attacks on baited lodgepole pine, *P. contorta* Dougl. ex Loud., trees, on unbaited trees adjacent to these trees (Huber and Borden 2001b), and within *P. contorta* stands (Borden et al. 2003).

The objectives of this study were to determine the effect of several green leaf volatiles, bark volatiles, and verbenone on *D. brevicomis* response to aggregation pheromone components within the central portion of its native range and to determine the most disruptive blend for reducing aggregation to attractant-baited traps.

Materials and Methods

Study Sites. Two trapping bioassays were conducted at McCloud Flats, Shasta-Trinity National Forest, Siskiyou County, California (41.35° N, 121.95° W; 1,150-m elevation) during 12–21 June (experiment 1) and 11–20 August (experiment 2) 2004. The stand was dominated by *P. ponderosa* (mean diameter at 1.37 m ± SEM, 35.8 ± 3.6 cm) growing on soils of volcanic origin. Mean stand density was 31.5 m² of basal area per hectare of which 95.5% was *P. ponderosa* with the remainder represented mainly by incense cedar, *Calocedrus decurrens* (Torr.) Florin; white fir, *Abies concolor* (Gond. & Glend.) Hildebr; Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; California black oak, *Quercus kelloggii* Newb.; and quaking aspen, *Populus tremuloides* Michx. Mean crown cover was 27%. The topography was mainly flat.

Experimental Design and Treatments. Twenty-seven (experiment 1) or 36 (experiment 2) 16-unit multiple funnel traps (Lindgren 1983) (Phero Tech Inc., Delta, British Columbia, Canada) were deployed along a forest road. Trap locations were separated by 25–30 m to avoid interference among adjacent treatments. Traps were hung on 3-m metal poles with collection cups 80–100 cm above the ground. Each trap location was randomly assigned one of nine (experiment 1) or 12 (experiment 2) treatments. A 3 by 3-cm time-released insecticidal Prozap Pest Strip (2,2-dichlorovinyl dimethyl phosphate, Loveland Industries Inc., Greely, CO) was placed in the collection cup to kill arriving insects and to reduce damage or loss to predacious insects. Samples were collected, and each treatment was rerandomized (three replicates per treatment per 24 h) daily between 0630 and 1000 hours to avoid disturbing traps during periods of peak flight activity (Fettig et al. 2004). Catches were immediately transported to the laboratory for storage and analysis. Specimens were tallied and identified using available keys (Wood 1982) and voucher specimens.

Nine nonhost angiosperm volatiles were selected for inclusion in this study based on their ubiquitous sensory activity in North American Scolytidae, particularly in *Dendroctonus* spp. (Huber et al. 2000b), their behavioral activity in *D. brevicomis* (Poland et al. 1998), and other bark and ambrosia beetles (Dickens et al. 1992; Schroeder 1992; Schlyter et al. 1995; Wilson et al. 1996; Borden et al. 1997, 1998; Guerrero et al. 1997; Byers et al. 1998, 2000; Deglow and Borden 1998a, b; Poland et al. 1998; Huber et al. 1999, 2000a, 2001; Zhang et al. 1999, 2001; Poland and Haack 2000; Schlyter et al. 2000; Huber 2001; Huber and Borden 2001a, 2001b, 2003; Zhang 2001, 2003). These volatiles were benzyl alcohol, benzylaldehyde, *trans*-conophthorin, guaiacol, nonanal, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol, and salicylaldehyde. These compounds are present in angiosperm trees indigenous to California in the range of *D. brevicomis*, including aspen and poplar (*Populus* spp.), birch (*Betula* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), and willow (*Salix* spp.) (Zhang and Schlyter 2004). Details concerning the source, purity, enantiomeric purity (if

Table 1. Description of semiochemicals and release devices used in trapping bioassays, Shasta-Trinity National Forest, Siskiyou County, California, 2004

Semiochemical	Source[a]	Purity (%)	Release device[b]	Release rate (mg/24 h)[c]
(E)-2-Hexenal	Bedoukian Research	97	Phero Tech bubblecap	3.5 (20°C)
(E)-2-Hexen-1-ol	Bedoukian Research	98	Phero Tech bubblecap	3.8 (20°C)
(Z)-2-Hexen-1-ol	Bedoukian Research	95	Phero Tech bubblecap	3.8 (20°C)
Benzyl alcohol	Fisher Scientific	98	Phero Tech bubblecap	1.3 (20°C)
Benzylaldehyde	Fisher Scientific	>99	Phero Tech flexure	3.5 (20°C)
trans-Conophthorin (racemic)	Phero Tech	87	0.4-ml Polyethylene vial	3.0 (28°C)
Guaiacol	Sigma-Aldrich	>98	Phero Tech bubblecap	5.0 (20°C)
Nonanal	Sigma-Aldrich	95	Phero Tech flexure	3.5 (20°C)
Salicylaldehyde	Sigma-Aldrich	99	Phero Tech bubblecap	5.0 (20°C)
Verbenone [80%-(−)]	Phero Tech	>97	Phero Tech bubblecap	4.0 (30°C)
Verbenone [82%-(−)]	Phero Tech	97	Phero Tech pouch	50.0 (30°C)
Frontalin (racemic)	Phero Tech	98	250-μl Eppendorf vial	3.0 (24°C)
exo-Brevicomin (racemic)		97	250-μl Eppendorf vial	3.0 (24°C)
Myrcene		90	1.8 ml × 2 Eppendorf vials	18.0 (24°C)

[a] Bedoukian Research, Bedoukian Research Inc., Danbury, CT; Fisher Scientific, Fisher Scientific International Inc., Liberty Lane, Hampton, NH; Phero Tech Inc., Delta, British Columbia; Sigma-Aldrich, and Sigma-Aldrich Canada Ltd., Oakville, Ontario, Canada.
[b] All release devices loaded by Phero Tech Inc.
[c] Measured in the laboratory at specified temperature.

chiral), release device, and release rate for each semiochemical are provided in Table 1.

Experiment 1 was conducted to determine the effects of verbenone, green leaf volatiles (GLV), bark volatiles (BV), and their combination (NAV) on *D. brevicomis* response to attractant-baited traps. The treatments included 1) unbaited control, 2) western pine beetle attractant (WPB; frontalin [racemic], *exo*-brevicomin [racemic], myrcene), 3) low release rate verbenone (LV; 80%-(−); 4.0 mg/24 h) + WPB, 4) GLV [(E)-2-hexenal, (E)-2-hexen-1-ol, (Z)-2-hexen-1-ol] + WPB, 5) BV (benzyl alcohol, benzaldehyde, conopthorin, guaiacol, nonanal, salicylaldehyde) + WPB, 6) NAV (=GLV + BV) + WPB, 7) GLV + LV + WPB, 8) BV + LV + WPB, and 9) NAV + LV + WPB. The experimental design was completely randomized with nine treatments and 30 replicates per treatment.

Experiment 2 was conducted to determine the effect of different release rates of verbenone, the alcohol (ALC) and aldehyde (ALD) fractions of the NAV blend, and *trans*-conophthorin (C) on *D. brevicomis* attraction. The effect of *trans*-conophthorin was determined through subtractive assay (Byers 1992). The treatments included 1) unbaited control, 2) WPB, 3) LV + WPB, 4) high release rate verbenone (HV; 82%-(−); 50.0 mg/24 h) + WPB, 5) ALC [(E)-2-hexen-1-ol, (Z)-2-hexen-1-ol, benzyl alcohol, guaiacol] + LV + WPB, 6) ALD [(E)-2-hexenal, benzaldehyde, nonanal, salicylaldehyde] + LV + WPB, 7) ALC + HV + WPB, 8) ALD + HV + WPB, 9) NAV + LV + WPB, 10) NAV-C + LV + WPB, 11) NAV + HV + WPB, and 12) NAV-C + HV + WPB. The experimental design was completely randomized with 12 treatments and 30 replicates per treatment.

Trap catches from unbaited controls were excluded from statistical analyses because of the heteroscedasticity among treatments that they caused (Reeve and Strom 2004). A test of normality was performed and appropriate transformations were used when the data

deviated significantly from a normal distribution (square root; Sokal and Rohlf 1995). A two-way analysis of variance (ANOVA) (treatment and sex) was performed on the number of *D. brevicomis* caught per trap per day using $\alpha = 0.05$ (SigmaStat version 2.0, SPSS Inc., Chicago, IL). Differences in the sex ratio of *D. brevicomis* caught among treatments, including the unbaited controls, were analyzed using a one-way ANOVA (lsmeans; SigmaStat version 2.0, SPSS Inc.). If a significant treatment effect was detected, the Tukey's multiple comparison test (Tukey's honestly significant difference [HSD]) was used for separation of treatment means.

Results

Experiment 1. In total, 23,783 *D. brevicomis* were captured in multiple funnel traps over the 10-d period. Overall, the ratio of males to females was 0.52. There was no significant treatment × sex interaction ($F_{7, 464} = 0.52; P > 0.82$); therefore, results pertain equally to both male and female responses. A significant treatment effect was observed ($F_{7, 232} = 9.35; P < 0.001$), and subsequent tests for normality ($P = 0.012$) and equal variance ($P = 0.027$) based on transformed data were acceptable. Sex ratios (M:F) for individual treatments ranged from 0.50 to 0.93 (GLV + LV + WPB and unbaited control, respectively). There were no significant differences in sex ratios among treatments ($F_{8, 222} = 1.05; P = 0.39$).

The BV, GLV, and NAV blends alone did not significantly affect the response of *D. brevicomis* to attractant-baited traps at the release rates included in this study (Fig. 1). Low release rate verbenone (LV; 4 mg/24 h) alone significantly reduced *D. brevicomis* attraction to attractant-baited traps by 46.9%. No significant differences in trap catch were observed among BV + WPB, GLV + WPB, NAV + WPB, and LV + WPB treatments (Fig. 1). The addition of the NAV blend to the LV + WPB treatment significantly
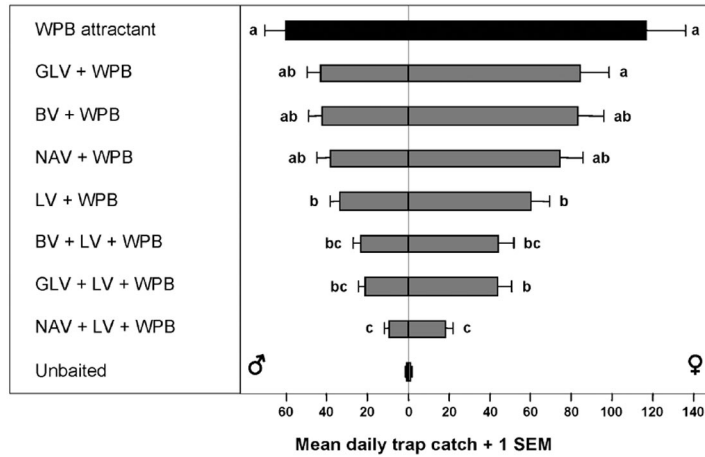
Fig. 1. Captures of *D. brevicomis* in multiple funnel traps baited with the *D. brevicomis* attractant, or with the attractant and a bark volatile blend (BV), a green leaf volatile blend (GLV), a nonhost angiosperm volatile blend (NAV), and verbenone (LV), Shasta-Trinity National Forest, Siskiyou County, California, 12–21 June 2004. WPB, three-component attractant; LV, verbenone [80%-(−)] (4 mg/24 h); GLV, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol; BV, benzyl alcohol, benzaldehyde, *trans*-conophthorin, guaiacol, nonanal, salicylaldehyde; and NAV, GLV + BV. Bars followed by the same letter are not significantly different ($n = 30$; Tukey's HSD; $P > 0.05$).

reduced trap catches below that of LV + WPB alone. The NAV + LV + WPB treatment resulted in a 70.5% reduction in trap catch compared with LV + WPB, and an 84.4% reduction compared with the positive control. Very few beetles (57) were collected in the unbaited traps.

Experiment 2. In total, 20,795 *D. brevicomis* were captured in multiple funnel traps over the 10-d period. Overall, the ratio of males to females was 0.43. There was no significant treatment × sex interaction ($F_{10,638} = 0.36$; $P > 0.96$); therefore, results pertain equally to both male and female responses. A significant treat-

ment effect was observed ($F_{10, 319} = 18.78$; $P < 0.001$), and subsequent tests for normality ($P = 0.06$) and equal variance ($P = 0.08$) based on transformed data were acceptable. Sex ratios (M:F) for individual treatments ranged from 0.38 to 1.02 (NAV + LV + WPB and unbaited control, respectively). A significant difference in sex ratios was observed among treatments ($F_{11, 295} = 3.51$; $P < 0.001$).

All treatments significantly reduced the response of *D. brevicomis* to attractant-baited traps (Fig. 2). There was no significant difference between the two release rates of verbenone. ALD did not significantly augment
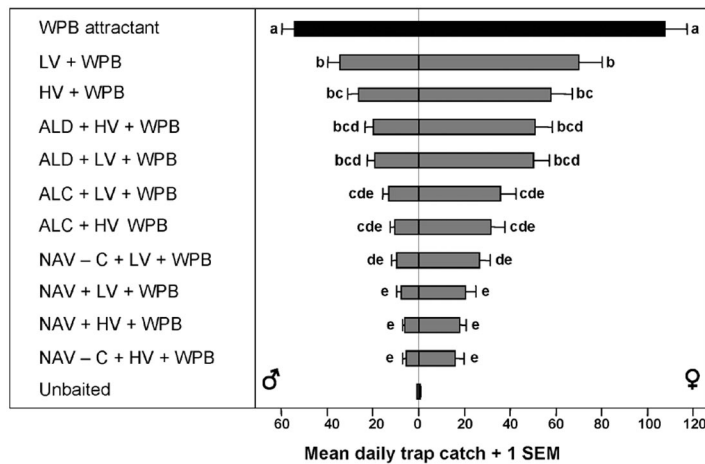

Fig. 2. Captures of *D. brevicomis* in multiple funnel traps baited with the *D. brevicomis* attractant, or with the attractant and an alcohol blend (ALC), an aldehyde blend (ALD), a nonhost angiosperm volatile blend (NAV), and verbenone (LV or HV), Shasta-Trinity National Forest, Siskiyou County, California, 11–20 August 2004. WPB, three-component attractant; LV, verbenone [80%-(−)] (4 mg/24 h); HV, verbenone [82%-(−)] (50 mg/24 h); ALC, benzyl alcohol, guaiacol, (*E*)-2-hexen-1-ol, (*Z*)-2-hexen-1-ol; ALD, benzaldehyde, nonanal, salicylaldehyde, (*E*)-2-hexenal; NAV, ALC + ALD + C; and C, *trans*-conophthorin. Bars followed by the same letter are not significantly different ($n = 30$; Tukey's HSD; $P > 0.05$).

the activity of either release rate of verbenone. The addition of ALC to LV + WPB significantly reduced attraction. There was a 49.6% reduction in trap catch when ALC was added to HV + WPB, but this effect was not statistically significant. No significant differences were observed between ALD + WPB and ALC + WPB in the presence of either release rate of verbenone. There were no significant differences in trap catch between ALC fractions and the complete NAV blend. The NAV-C + HV + WPB treatment had the lowest trap catch (exclusive of unbaited control), indicating that *trans*-conophthorin can be removed from the NAV + HV mixture without any loss of behavioral activity. The NAV-C + HV + WPB treatment resulted in a 74.4% reduction in trap catch compared with HV + WPB, and an 86.7% reduction compared with the attractant-baited control. Very few beetles (36) were collected in the unbaited traps.

Discussion

This is the first report on the effects of several bark volatiles (benzyl alcohol, benzaldehyde, *trans*-conophthorin, guaiacol, nonanal, and salicylaldehyde), green leaf volatiles [(*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-2-hexen-1-ol], and nonhost angiosperm volatile-verbenone blends on *D. brevicomis* attraction (Zhang and Schlyter 2004). These blends did not significantly affect the response of *D. brevicomis* to attractant-baited traps (Fig. 1). However, NAV augmented the disruptive effect of 4 and 50 mg/24-h verbenone to levels significantly below that of verbenone alone (Figs. 1 and 2). It is possible that the NAV blend reduced attraction in a portion of the *D. brevicomis* population and that the remaining portion (i.e., beetles that were not as responsive to the NAV blend) was disrupted more strongly by verbenone. Such a relationship would help explain the effect observed in this study when NAV and LV were combined (Fig. 1). Alternatively, and perhaps more probable, is that verbenone and the other NAV compounds work together simultaneously at the antennal level to inhibit attraction. In this instance, the probability of any given beetle to respond to the attractant is reduced because of the combined action of these compounds on its antennal receptors. Similarly, it has been demonstrated that green leaf volatiles and verbenone significantly reduced *Ips typographus* (L.) attraction beyond that of either compound alone (Zhang 2003, Zhang and Schlyter 2003). The addition of nonhost angiosperm volatiles to verbenone also permits exploitation of a larger number of ecological interactions than verbenone alone (Borden 1997, Zhang and Schlyter 2004).

This population of *D. brevicomis* was not as behaviorally responsive to nonhost angiosperm volatiles as are several other bark beetle species, including many congenerics (Poland et al. 1998, Huber et al. 2000a, Huber and Borden 2001a, Zhang and Schlyter 2004). Our results indicate that the NAV blend examined here is not effective for reducing *D. brevicomis* attraction to attractant-baited traps in the absence of ver-

benone (Fig. 1). Poland et al. (1998) reported that the green leaf aldehyde (*E*)-2-hexenal and the two green leaf alcohols (*E*)-2-hexen-1-ol and (*Z*)-2-hexen-1-ol significantly reduced male, but not female attraction. The greatest disruptive effect, compared with the attractant-baited control, observed in that study was 46.7% (Poland et al. 1998). During experiment 1, we observed a 36.3% reduction in total trap catch with our NAV blend compared with the attractant-baited control, but that effect was not statistically significant (Fig. 1). The (*E*)-2-hexenal tested by Poland et al. (1998) was released at a 3.7× higher rate (13 mg/24-h release rate) than in this study. It is possible that a significant treatment effect may have been observed if we had increased the release rate of this green leaf volatile (Table 1).

Our selection of nonhost angiosperm volatiles was based solely on a previous trapping bioassay (Poland et al. 1998), and on electroantennograph detection (EAD) analysis (Huber et al. 2000b) and trapping data for other scolytids (Dickens et al. 1992; Schroeder 1992; Schlyter et al. 1995, 2000; Wilson et al. 1996, Borden et al. 1997, 1998; Guerrero et al. 1997, Byers et al. 1998, 2000; Deglow and Borden 1998a, b; Poland et al. 1998, Huber et al. 1999, 2000a, 2001; Zhang et al. 1999, 2001; Poland and Haack 2000, Huber 2001, Huber and Borden 2001a, b, 2003; Zhang 2003). No EAD data concerning *D. brevicomis* detection of angiosperm volatiles exists, so it cannot be said with certainty that the species can detect each of the individual volatiles examined here. The ALC fractions of the NAV blend seem to be more important than the ALD fractions for disrupting the response of *D. brevicomis* to attractant-baited traps because the mean trap catch in ALC + LV + WPB traps was significantly lower than traps with LV + WPB (Fig. 2).

Conophthorin is known to be antennally active to a variety of bark beetles, including *Dendroctonus* spp. (Zhang and Schlyter 2004), and disrupts positive chemotactic responses of *D. ponderosae*, *D. pseudotsugae* (Huber et al. 1999), *Dryocoetes confusus* Swaine (Huber 2001), *Ips cembrae* (Heer) (Zhang 2001), *Ips duplicatus* (Sahlberg) (Zhang et al. 2001), *Ips pini* (Say) (Huber et al. 1999), *Ips perturbatus* (Eichhoff) (A. Graves, University of Minnesota, personal communication), and *I. typographus* (Zhang et al. 2001). This bark volatile is also a male-produced antiaggregation pheromone of several scolytids, including *Conophthorus* spp. (Birgersson et al. 1995, Pierce et al. 1995), and it is an attractant produced by *Pityophthorus* spp. (Dallara et al. 2000). The synthesis of conophthorin is expensive and conophthorin is often difficult to procure. Our results indicate that *trans*-conophthorin is not vital to the efficacy of our NAV blend for reducing *D. brevicomis* aggregation to attractant-baited traps.

Dudley (1971) reported that *D. brevicomis* sex ratios during gallery formation do not differ significantly from unity. In our study, the sex ratios observed in unbaited traps are similar to those reported for mass attack, gallery formation, and emergence (Miller and Keen 1960, Dudley 1971). The attractant significantly increased the ratio in favor of females in experiment

2, but not experiment 1. There were no significant differences among sex ratios between the attractant and other treatments containing nonhost angiosperm volatiles, indicating that both male and female portions of the population are equally responsive to nonhost angiosperm volatiles. This is of practical importance as females initiate host colonization, and their disruption in an operational semiochemical-based pest management tactic would be critical to achieving success. Disruption of males would reduce mating opportunities for any unresponsive females as well.

Tilden and Bedard (1988) showed that low release rates of verbenone (<1.0 mg/24 h) are ineffective for reducing aggregation in *D. brevicomis.* Captures of *D. brevicomis* were significantly reduced by verbenone [86%-(−)] released at 6.0 and 30.0 mg/24 h in attractant-baited traps (Bertram and Paine 1994). Tilden and Bedard (1988) reported that 4.7, 61.4, and 613.8 mg/24 h verbenone [60%-(+)] significantly reduced *D. brevicomis* attraction to traps baited with *exo*-brevicomin (8.4 mg/24 h), frontalin (1.6 mg/24 h), and myrcene (700.3 mg/24 h) and that trap catch was inversely related to release rate. In our study, no significant difference was observed between the mean trap catch of 4 and 50 mg/24 h verbenone [80%-(−)] (Fig. 2). This suggests that general increases in the release rates of verbenone are not always associated with decreases in *D. brevicomis* trap catches as has been suggested by other authors (Bedard et al. 1980a, Tilden and Bedard 1988). Differences are likely influenced by the stereochemistries and release rates of both the attractant (positive control) and verbenone used in these behavioral assays.

An understanding of the ecological and physiological aspects of host selection and colonization is critical to the development of semiochemical-based management tactics for bark beetle control. There continues to be considerable need and interest in the development of such tools. Further investigations will allow us to improve and refine our NAV blend and will help facilitate the development of an effective tool for protecting *P. ponderosa* from *D. brevicomis* infestations.

Acknowledgments

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